Recovery Planning and Reintroduction of the Federally Threatened Pitcher's Thistle (*Cirsium pitcheri*) in Illinois

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ABSTRACT: Pitcher's thistle (*Cirsium pitcheri*) is a narrowly distributed endemic of the western Great Lakes shorelines. This monocarpic herb is an obligate colonizer of >70% open sand habitat in early- to mid-successional vegetation maintained by intermediate levels of disturbance or created by stochastic disturbance events. Its persistence can be modeled within a metapopulation framework, where interacting populations react to environmental factors independently, facilitating metapopulation persistence. The habitat requirements of Pitcher's thistle have made it extremely vulnerable to shoreline erosion, development, and recreational use. It is federally listed as threatened and state listed as endangered or threatened throughout its range in the United States.

In Illinois, Pitcher's thistle was collected at least twelve times from the Lake Michigan shoreline between 1862 and 1919; it then apparently disappeared, probably as a result of the combined effects of increasing human activity, lake level fluctuations, collecting, and other chance events. Restoration of *Cirsium pitcheri* in Illinois is an objective of the federal recovery plan, and Illinois Beach State Park contains the only remaining Illinois dune systems where it might be reintroduced. To identify appropriate restoration habitat, the vegetation at Illinois Beach was compared to the nearest occupied *Cirsium pitcheri* habitats, at Indiana Dunes National Lakeshore and at Kohler-Andrae State Park in Wisconsin. Ordination and cluster analysis demonstrated strong similarities between upper beach, foredune, secondary dune, and dunefield habitat in Illinois and similar thistle-occupied habitats in Indiana and Wisconsin. However, at Illinois Beach State Park only the secondary dune habitat appeared to be free from shoreline erosion and recreational impacts. Propagated plants from Indiana and Wisconsin seed sources were introduced into this habitat in 1991, with greater survivorship among the Indiana plants. Experimental establishment of additional cohorts from seeds and propagated material is needed to further identify appropriate microhabitat, while shoreline protection, control of recreation, and periodic reintroduction may be required to maintain a metapopulation at Illinois Beach.

INTRODUCTION

The federal Endangered Species Act (of 1973) calls for planning and implementing the recovery of listed species so that they are no longer threatened or endangered with extinction. Many federal recovery plans for plants have focused on protecting existing populations, avoiding the often difficult or delicate issue (e.g., Fahselt 1988) of restoring former or introducing new populations. Even though restoration may not be necessary in the recovery of all species, attempts to restore a species to a part of its former range may be critical in determining if the factors that caused its decline can be ameliorated or overcome, and if the species can indeed be recovered and delisted. Criteria for plant population restoration should include assessment of the species' ecological requirements (DeMauro 1993a, Pavlik et al. 1993, Pavlovic 1993), its breeding system and reproductive requirements (DeMauro 1993b, Weller 1993), the genetic source of propagules (Hamrick et al. 1991), an appropriate experimental design for planting and demographic monitoring (Travis and Sutter 1986, Pavlik 1993), and legal protection of restoration habitat.

Pitcher's thistle (*Cirsium pitcheri* [Torrey ex Eaton] T. & G.) is a western Great Lakes shoreline endemic that is listed as threatened in the United States (Harrison 1988) and rare in Ontario (White et al. 1983). Most extant U.S. populations are found in Michigan, which has more than 120 occurrences. Ten populations occur in three Wisconsin counties, and six populations remain in Indiana. There were at least three historic populations in Illinois, where the plant has not been found since 1919. Because of its decline in the southern part of its range, the federal recovery plan (Pavlovic et al. 1992) calls for population restoration in Illinois. This paper reviews the ecology and former Illinois distribution of *C. pitcheri* and describes the methodology and preliminary results of its reintroduction to Illinois.

SPECIES BACKGROUND

Distribution and Ecology

Cirsium pitcheri once had a nearly continuous distribution along the beaches and dunes of Lake Michigan in Wisconsin, Illinois, Indiana, and Michigan. It occurred less frequently along the Michigan and Ontario borders of Lake Huron, and rarely along Lake Superior's north shore in Ontario and its south shore in Michigan (Figure 1; Guire and Voss 1963, Keddy and Keddy 1984).

This species is believed either to have originated in the Great Plains and migrated eastward along the glacial boundary to its present habitat (Moore and Frankton 1963), or to have originated from a founder event in the Great Lakes region (Johnson and Iltis 1963). It is closely related to the western Platte thistle (*Cirsium canescens* Nutt.), and both share a common chromosome number of 2n = 34 (Ownbey and Hsi 1963). However, Loveless and Hamrick (1988) found *C. pitcheri* to possess lower genetic variation and also found a negative correlation between genetic similarity and distance separating five geographic groups (Lower Michigan, Indiana, Straits of Mackinac, Upper Peninsula of Michigan, and upper Wisconsin). Thus, the Pitcher's thistles formerly present in Illinois were probably most closely related to those of southern Wisconsin, northern Indiana, and, possibly, southwestern Michigan.

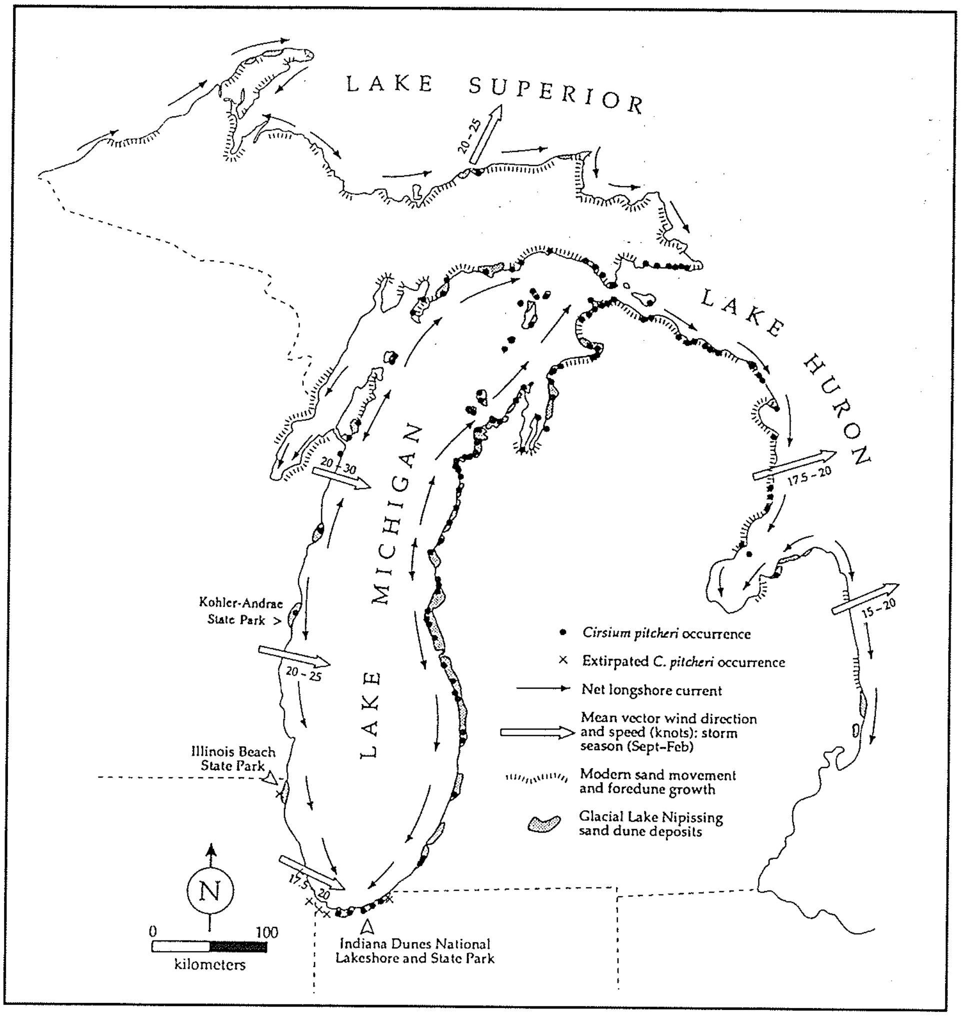

Figure 1. ***Cirsium pitcheri*** **species and habitat distribution dynamics of western Great Lakes dune systems (redrawn from Hands 1970, Dorr and Eschman 1971, Bird and Schwartz 1985, Saulesleja 1986, Pavlovic et al. 1992).**

Lake Michigan shoreline vegetation forms a series of early- to late-successional stages (Cowles 1899) across a typical zonation of beach, foredune, interdunal swale, and secondary dunes with gradients of increasing dune age and decreasing wind disturbance (Olson 1958). This vegetation continuum shifts in time and space as shorelines undergo erosion and accretion cycles with lake level fluctuations (McEachern 1992). *Cirsium pitcheri* is highly dependent on open grassland conditions created by shoreline disturbances, within which it requires 70% or more open sand for seedling establishment and survival (McEachern 1992). It is usually absent from rapidly forming or fully vegetated dunes, and its persistence depends on its colonizing the mosaic of transient microhabitats of dynamic dune systems. Appropriate microhabitats are either maintained by intermediate disturbance levels on upper beaches, foredunes, and windward slopes of secondary dunes, or persist through the mid-successional vegetation stage in blowouts. Succession or stochastic disturbances can eliminate local habitats and thistle populations, while disturbances can also create new habitats that can be colonized by thistles (McEachern 1992). The shifting habitat dynamics of coastal dune complexes thus require that *C. pitcheri* have metapopulation dynamics (McEachern et al. 1993). Metapopulations consist of interacting populations that persist in spatially and temporally variable environments where the probability of local extinction is high (Gilpin and Hanski 1991). For metapopulations to persist, local populations must avoid simultaneous extinction by reacting independently to landscape-scale disturbances and colonizing newly formed habitats.

Life History

Cirsium pitcheri is a monocarpic perennial herb with no capacity for vegetative spread; plants flower at approximately five to eight years of age, disperse seed, and then die (Loveless 1984, Loveless and Hamrick 1988). Thus if populations are to persist or colonize new habitat patches, they must produce seeds and establish seedlings. It is unknown if this thistle maintains a seed bank; it has a mixed mating system, with 35-88% outcrossing through insect pollinators (Keddy and Keddy 1984, Loveless 1984). Although it is partly self-compatible and capable of self-pollination, outcrossed and open-pollinated heads have higher seed set (Loveless 1984). Thus populations established by single founders would benefit from continued immigration.

Seeds of *Cirsium pitcheri* are the largest of any northeastern North American thistle (Gleason 1952); they mature in late summer, apparently remain dormant until moist-stratified, and germinate the following spring. Often, few mature seeds are successfully produced or dispersed because of predispersal predation by the larvae of plume moths (Keddy and Keddy 1984) and postdispersal predation by various birds (particularly goldfinches) and, possibly, small mammals (Loveless 1984). The pappus easily detaches, and dispersal of the relatively heavy seeds is generally within 4 m of the parent plant (McEachern 1992). Seeds are also retained in flower heads on senescing plants, which results in aggregations of seedlings near the former locations of adults.

Impacts and Threats to *Cirsium pitcheri*

For disturbance-dependent plants, timing and frequency of disturbance are critical to population persistence (Pavlovic 1993). Although *Cirsium pitcheri* is adapted to a dynamic habitat, it may be susceptible to disturbances that occur out of phase or with higher frequency, severity, or magnitude than natural site disturbances. In general, habitat disturbances that occur more frequently than thistle reproduction, especially those that consistently remove cohorts or prevent seed production, could cause thistle populations to decline and eventually become extinct (McEachern 1992).

A direct threat to Pitcher's thistle is habitat destruction by human activities such as sand mining, shoreline development, or attempts to stabilize dunefields and shorelines with plantings. A serious indirect human threat is physical shoreline stabilization by jetties, rip-rap, or retaining walls. This prevents longshore currents from moving and replenishing sand (Larsen 1985) and exacerbates shoreline erosion during periods of high lake levels and severe winter storms (Wood and Davis 1987). Under such conditions, Pitcher's thistle does not occupy beach habitat but often survives in blowouts in adjacent inland dune complexes (Bowles et al. 1990, McEachern 1992, McEachern et al. 1993).

In Wisconsin, Dobberpuhl and Gibson (1987) found that human recreation in thistle habitat can have potentially long-term negative effects on thistle populations. Juvenile and seedling thistles are highly vulnerable to trampling; this can eliminate cohorts, thereby causing a distorted size class distribution and a declining population growth rate. Moderate recreational use may also help maintain local thistle habitats by retarding succession. For example, at one Wisconsin site populations expanded into foredune habitat in which human trampling apparently mimicked natural low-level disturbance. However, such impacts are usually linear and spatially fixed and if intensified, may eventually impact thistle populations.

DECLINE OF *CIRSIUM PITCHERI* IN ILLINOIS

Former Illinois Habitats

Twelve Illinois collections of Pitcher's thistle are known from the Lake Michigan Shoreline of Cook and Lake counties between 1862 and 1919; but these provide only vague habitat information such as "sand hills," "shore," "dry sand beaches," "sand," "sandy shore," and "lakeshore," usually near Waukegan or Chicago (Pavlovic et al. 1992). Early literature that mentions *Cirsium pitcheri* (Beal 1871, Babcock 1872, Higley and Raddin 1891) is similarly vague, although Warne (1870) described the plants as occurring with *Opuntia* on sandy ridges along the lakeshore north of Chicago. In an area that is now within the southern half of Illinois Beach State Park, Gates (1912) described the habitat of *Cirsium pitcheri* as the "*Artemisia-Panicum* association of the Upper Beach Association" of Cowles (1899). This area was "30-40% unvegetated, and dominated by *Artemisia caudata* (ranging from 30-50% cover), *Panicum virgatum*, and *Sporobolus cryptandrus*." Gates categorized *C. pitcheri* as a "Secondary Species" in association with *Lathyrus japonicus*, *Euphorbia polygonifolia*, *Lithospermum croceum*, *Arenaria stricta*, *Cycloloma atriplicifolium*, *Equisetum hyemale*, *Arabis lyrata*, and *Petalostenum purpureum*. Gates found only four thistles and apparently collected three of them (while accompanied by H.A. Gleason)! Although Cowles (1899) indicated that Pitcher's thistle also occurred in dunes adjacent to and inland from the beach, Gates did not record this species from dunes or from an adjacent bunch-grass association, even though it was 60-75% unvegetated (Gates 1912). H.S. Pepoon, who accompanied Gates during his fieldwork in 1908, did not mention *Cirsium pitcheri* in his lengthy discussion of the area studied by Gates (Pepoon 1927), and neither did Atwell (1932) in a brief sketch of the same area.

Causes of Extirpation

Populations can be extirpated through demographic stochasticity — chance events in the survival and reproduction of individuals (which are critical in small populations); environmental stochasticity — temporal changes in habitat and environment; natural catastrophes; and genetic stochasticity — loss of fitness due to genetic changes (Shaffer 1981, Wilcox and Murphy 1985, Gilpin and Soulé 1986). The extirpation of *Cirsium pitcheri* from Illinois could have involved all four factors, with interactions between increasing human impact, lake level fluctuations, and chance events affecting populations that were already small and within a narrow habitat.

Because thistles were collected over a 58-year period (1862–1919) along Lake Michigan in Illinois, reproducing populations were apparently present. Blowouts were probably rare in those low dune habitats, with thistle metapopulations dependent on a narrow, shifting successional gradient between the beach, foredune, and secondary dune system, and on migrations parallel to the lakefront. This would have left populations vulnerable to natural and human-exacerbated shoreline erosion during the high lake levels of the 50 years prior to

1900 (Gates 1912) (Figure 2). Later, during lower lake levels, construction in Chicago and increased beach traffic and development between Chicago and Gary (Moore 1959) could have prevented migration and furthered thistle decline. It is unknown if overcollecting contributed to long-term decline of Pitcher's thistles, but the taking of three of the four plants observed by Gates in 1908 may have affected a declining population.

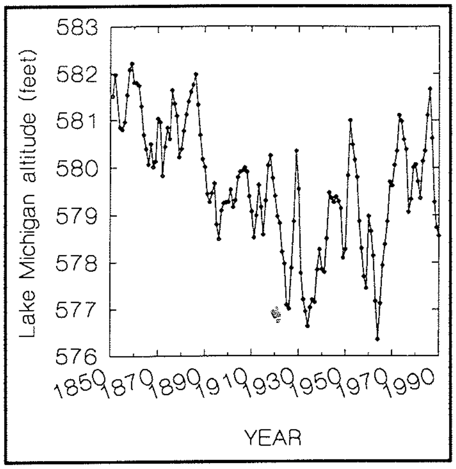

Figure 2. Lake Michigan fluctuations 1850–1990. Data provided by T. Thompson (Indiana Geological Survey), based on U.S. Army Corps of Engineers Great Lakes datum 1985.

RECOVERY PLANNING

Objectives and Criteria

Recovery planning for *Cirsium pitcheri* requires identification of appropriate dune system habitat in which ecological requirements of *C. pitcheri* are met, and in which a metapopulation framework can be used to link landscape and population processes (McEachern et al. 1993). This requires dynamic shoreline habitat of sufficient size and heterogeneity to prevent the population components of a metapopulation from being simultaneously affected by the same environmental processes. Sites selected for restoration should also have long-term management and protection, which would allow the processes of dune building, erosion, and plant succession to operate. Based on these criteria, the only remaining Illinois site for thistle restoration is Illinois Beach State Park. Reintroduction should replicate as closely as possible the habitat conditions, and the mixed mating system and genetic characteristics (sensu Loveless 1984), of extant thistle populations. Therefore, habitats and associated plant communities were studied at the sites nearest to Illinois Beach State Park containing *C. pitcheri* and from which a large sample of thistle seeds might be collected from multiple parents: Indiana Dunes National Lakeshore, Lake and Porter counties, Indiana, and Kohler-Andrae State Park, Sheboygan County, Wisconsin.

Site Descriptions

Illinois Beach State Park is located 70 km north of Chicago, on a 1.5-km-wide low (up to 3 m elevation) ridge and swale sand deposit extending 22.6 km along the Lake Michigan shoreline (Figure 3). This sand body is transient with the southward longshore current; it reaches a maximum age of 3500 years near the Illinois-Wisconsin state line (Larsen 1985), and the shoreline is eroding in the north and accreting toward the south. In comparison, beach ridges are compressed into a narrow dunefield north of the Dead River, but are more widely spaced as they accrete southward. The Lake Michigan shoreline position in this area also has fluctuated with cyclic lake level changes (Hester and Fraser 1973), and shoreline erosion has recently accelerated (Fraser and Hester 1974) as a result of high lake levels and exacerbation by blockage of longshore current sand transport from

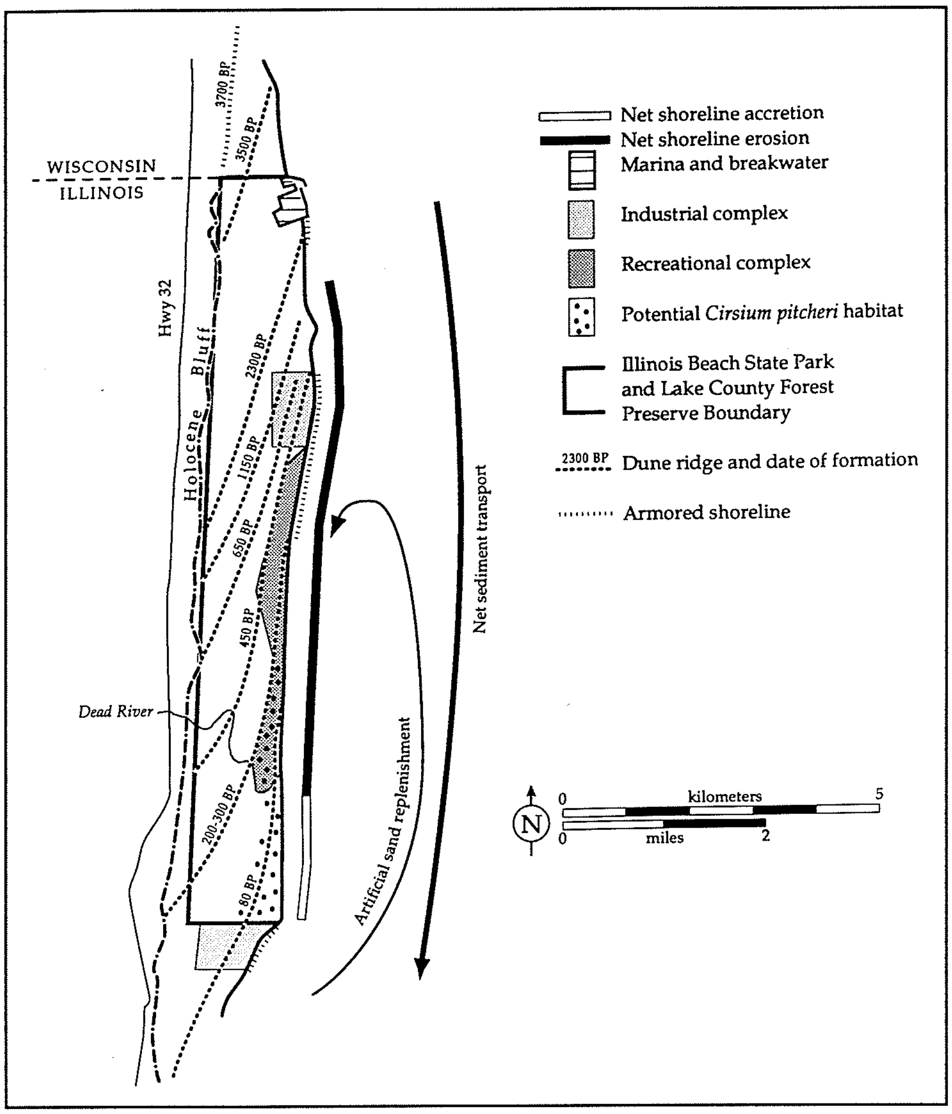

Figure 3. Shoreline dynamics and potential *Cirsium pitcheri* habitat at Illinois Beach State Park, Lake County, Illinois.

shoreline structures such as the Zion Marina and the Zion Nuclear Power Plant. This erosion is being ameliorated by periodic artificial sand replenishment south of the shoreline structures. Based on sand replenishment data, up to 300,000 m^3 of sand have been lost and replaced from Illinois Beach State Park over six years (Illinois Department of Conservation, pers. com.). Because it counteracts erosion, beach replenishment might appear beneficial to *C. pitcheri* recovery, but it is not beneficial if erosion and sand replenishment are too severe or too frequent for thistle persistence.

The Indiana and Wisconsin Lake Michigan shoreline dune systems are structurally different from those of Illinois (McEachern et al. 1993). The Indiana Dunes are formed in a much larger sediment deposit at the southern tip of Lake Michigan. These Nipissing-age dunes compose a high (up to 50 m elevation) dune complex extending more than 1 km inland, in which extensive blowouts are common. Although thistles formerly occupied beach habitat at the Indiana Dunes, their primary habitat now is in open blowouts of the high-dune complex (Bowles et al. 1990, McEachern 1992, McEachern et al. 1993). Thistle habitat at Wisconsin's Kohler-Andrae dune system consists of an approximately 100-m-wide zone of beach and foredune bordered by northern hardwood forest. The beach zone varies from 35 to 50 m wide, and the adjacent foredune merges into a dunefield that is approximately 50 m wide.

METHODS

Vegetation Sampling and Data Analysis

The southern part of Illinois Beach State Park contains the largest remaining high-quality area of protected Lake Michigan shoreline vegetation in Illinois (Illinois Nature Preserves Commission 1990). It was studied as thistle habitat because of its potential long-term stability. Two potential sites were investigated. One is a 100-m-wide zone of foredune and secondary dune system that extends for 1 km along the lakeshore. These dunes reach heights of 1.5 m above Lake Michigan. The second area is a 15-ha (c. 40-acre) dunefield with dunes reaching approximately 3 m in height. This area receives recreational use and is characterized by open disturbance patches.

In 1990, data on existing thistle habitat in Indiana and Wisconsin were collected from 100-m-long stratified random sampling transects. At Indiana Dunes National Lakeshore, six such transects were sampled through upper beach (1 transect), foredune (1 transect), secondary dune (1 transect), and blowout (3 transects) habitat. These data were supplemented by four additional blowout transects sampled at the Indiana Dunes in 1988. At Kohler-Andrae, single transects were established through upper beach and dunefield habitat containing thistles. For comparison, eight sampling transects were established at Illinois Beach. Seven were parallel to Lake Michigan across the 100-m-wide zone of upper beach, foredune, foredune slope, swale, secondary dune slope, secondary dune, and swale. The eighth transect was parallel to Lake Michigan through the dunefield. Species presence and cover, and open sand cover were quantified in 20 random 1-m^2 plots along these transects. Cover was estimated in eight classes: I >0-5%, II >5-15%, III >15-30%, IV >30-50%, V >50-70%, VI >70-85%, VII >85-95%, VIII >95-100%. Mean median cover values were summed into life-form (grass, forbs, and shrubs) and substrate (sand) groups for graphical comparison.

The transects were compared within each of the three study sites by direct gradient analysis of community structure (grass, forb, and shrub cover; species richness; and sand cover) in relation to topographic position and distance from the lakeshore. Relationships among sites were determined by ordination and classification on PC-ORD (McCune 1991). First, the habitat transects were treated as stands and ordinated by detrended correspondence analysis (DECORANA) of plant frequency data (provided in Table 1). DECORANA is an eigenvector ordination technique based on reciprocal averaging and aligns stands along strong environmental or successional gradients. Second, related stands were identified and grouped on the ordination axis by Ward's error sum of squares method of agglomerative cluster analysis. Ward's is a hierarchical classification technique that groups similar stands into a dendrogram. Species richness and the Shannon diversity index ($H' = -S(P_i \times \ln p_i)$) were calculated for each transect by PC-ORD.

Seed Collection, Propagation, Planting, and Data Analysis

Cirsium pitcheri seeds were collected by permit in 1990 from Kohler-Andrae State Park, Sheboygan County, Wisconsin, and from the Porter County, Indiana, portion of Indiana Dunes National Lakeshore. Seeds were removed from the standing dried inflorescences of a minimum of ten widely scattered plants after most seeds had naturally dispersed. Approximately 150 seeds were collected at each site, and approximately one-third of the seeds (50 per site) appeared viable. Seeds were moist-stratified on filter paper in Petri dishes for four months at 40°F and planted on April 1, 1991 in flats of potting soil composed of 90% torpedo sand (screened of particles >30 mm) and 10% silt loam (screened of particles >1.5 mm). To test for potential genetic differences between the Wisconsin and Illinois seed sources, we compared mean cotyledon width between the two seedling cohorts with a t-test. After mature leaves developed and cotyledons yellowed, the seedlings were transplanted to individual pots and greenhouse grown until they were outplanted on August 1, 1991.

Once planting habitat had been selected at Illinois Beach, four planting transects were extended east from a 100-m north-south baseline arbitrarily established on the secondary dune ridge at Illinois Beach (see following section). The four transects were separated by arbitrary distances (22 m, 15 m, and 30 m) and were planted with 21, 18, 18, and 21 thistles from the 1991 cohort. The first two transects were planted with alternating Indiana and Wisconsin plants, the third was planted with Indiana plants, and the fourth was planted primarily with Wisconsin plants. Each thistle was planted within 1 m of either side of each transect in areas that were at least 0.25 m from the nearest thistle and had >50% open sand. Before planting, the pot containing each plant was placed in a water-filled bucket shoreline structures such as the Zion Marina and the Zion Nuclear Power Plant. This erosion is being ameliorated by periodic artificial sand replenishment south of the shoreline structures. Based on sand replenishment data, up to 300,000 m^3 of sand have been lost and replaced from Illinois Beach State Park over six years (Illinois Department of Conservation, pers. com.). Because it counteracts erosion, beach replenishment might appear beneficial to *C. pitcheri* recovery, but it is not beneficial if erosion and sand replenishment are too severe or too frequent for thistle persistence.

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After initial planting on August 1, 1991, the plantings were monitored in May and September 1992. Two-by-two contingency tables were used to compare survivorship between mixed and unmixed planting transects, between east and west halves of each transect, and between the Indiana and Wisconsin 1991 cohorts in fenced and unfenced plantings. Additional morphological features, including leaf number, leaf length, and root crown width, have been measured for long-term comparisons of growth performance but are not reported in this paper.

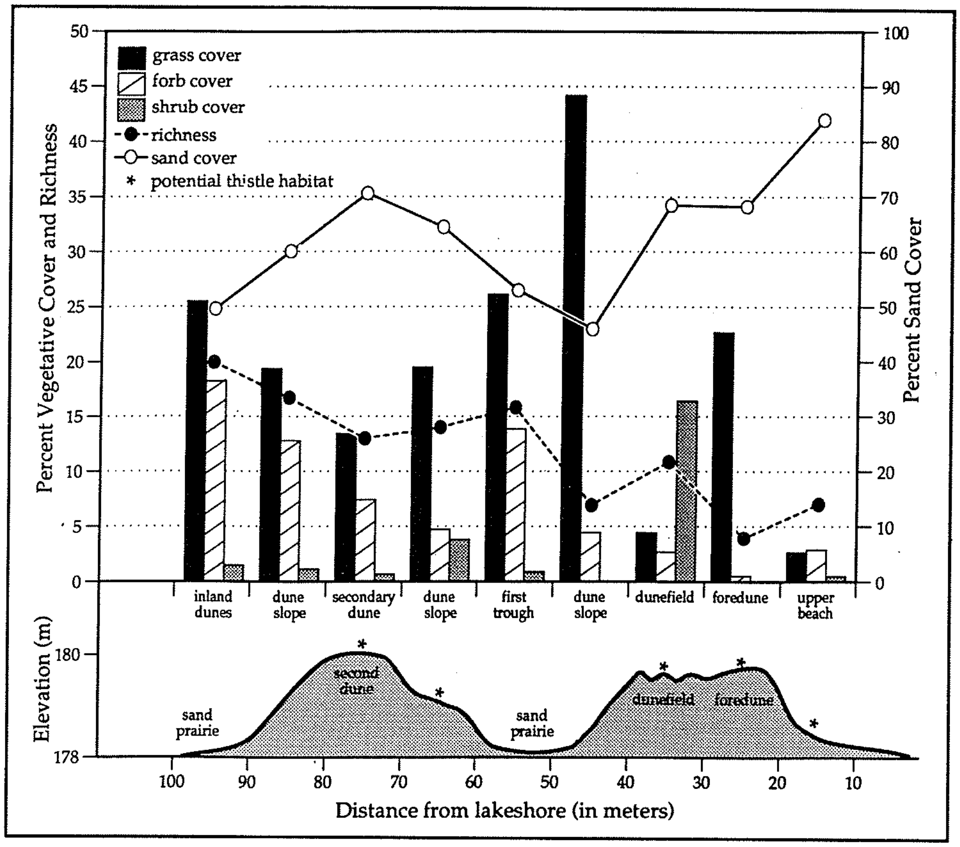

Figure 4. Change in plant community structure and potential *Cirsium pitcheri* habitat across a ridge and swale habitat gradient at Illinois Beach State Park, Lake County, Illinois.

RESULTS OF VEGETATION ANALYSIS

Within-site Characteristics

At Illinois Beach, open dune habitat extended inland up to 100 m through a dune series across the upper beach, foredune, dunefield, sand prairie, and a second dune and sand prairie (Figure 4). Sand cover approached or exceeded 70% on the upper beach and dune ridges and dropped below 50% in the dune swales. In sampling plots, grasses dominated the vegetation structure on the foredune and dune slopes but shared dominance with forbs in the species-rich sand prairie vegetation of the dune swales. The dunefield, which formerly supported *Pinus strobus* (Pepoon 1927), had >75% open sand in patches within a shrub matrix. Shrubs, primarily *Juniperus horizontalis* and *Arctostaphylos uva-ursi*, were the dominant vegetation in the dunefield, with 15% cover; grasses, primarily *Andropogon scoparius* and *Calamovilfa longifolia*, and forbs had <10% cover.

In the Indiana Dunes, open dune habitat extended 700 m inland from the upper beach, across the foredune, secondary dune, and a dune complex that contained a series of early-, mid- and late-successional blowouts (Figure 5). In sampling plots, grasses dominated the vegetation structure in all habitats, and shrub cover exceeded herbaceous cover only in the foredune. Sand cover reached >90% on the upper beach, was approximately 70% in intermediate beach habitats, and dropped to 30% in late-successional blowouts. In comparison, *Cirsium pitcheri* was absent from the upper beach and foredune, was most abundant in early to mid-successional secondary dunes and blowouts, and declined with advancing succession and decreasing sand cover in late-successional blowouts (McEachern 1992, McEachern et al. 1993; Table 1). In these habitats, *Calamovilfa longifolia* and *Andropogon scoparius* were the dominant vegetation, and common forbs included *Artemisia caudata*, *Solidago nemoralis*, and *Corispermum hyssopifolium*.

At Kohler-Andrae State Park, open dune habitat and *Cirsium pitcheri* were confined to a 100-m-wide zone of upper beach and an adjacent broad foredune or dunefield. In sampling plots, grasses dominated the vegetation structure in both habitats, but forb and shrub cover were relatively high in the beach and dunefield, respectively. Pitcher's thistle occured infrequently in the upper beach zone in more than 90% open sand in association with *Ammophila breviligulata*, *Lathyrus japonicus*, *Corispermum hyssopifolium*, and *Agropyron dasystachyum* (Table 1). However, thistles reached up to 35% frequency in the dunefield, which had 65% open sand in patches within a shrub matrix. Grasses, primarily *Calamovilfa longifolia*, were the dominant plants in the dunefield, with 20% cover; shrub cover was <10%, primarily from *Prunus pumila* and *Juniperus horizontalis*.

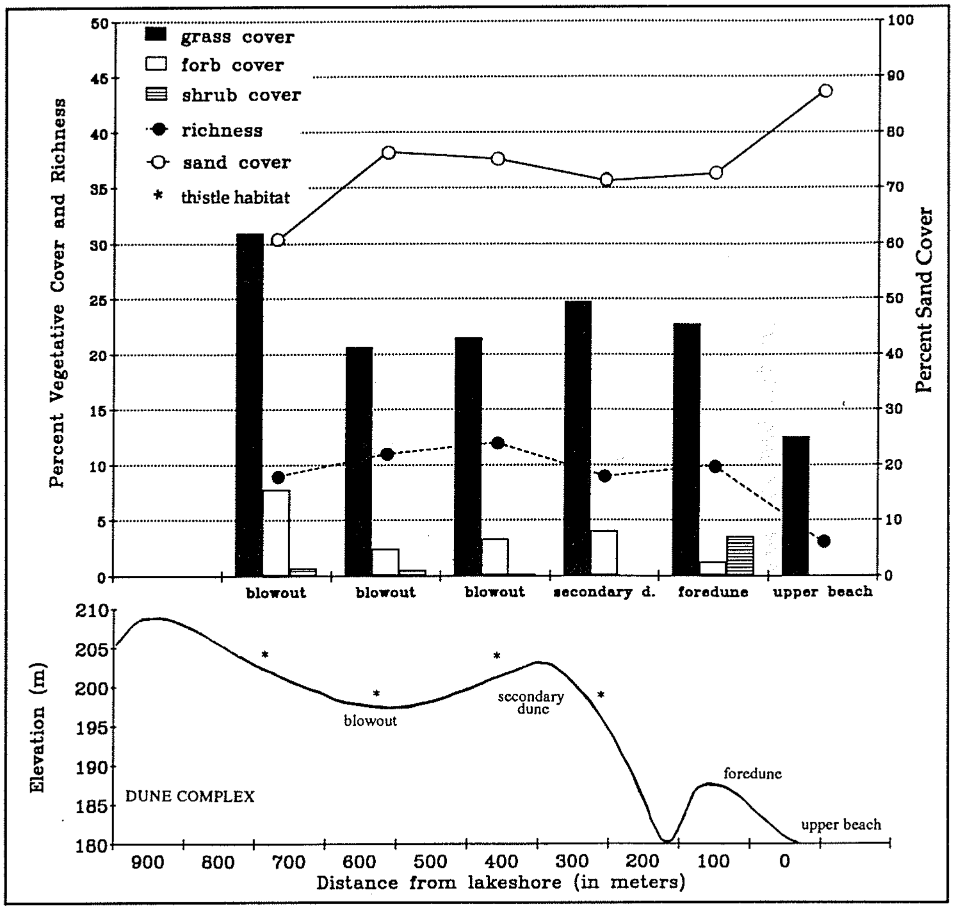

Figure 5. Change in plant community structure and *Cirsium pitcheri* habitat across a dune complex gradient at Indiana Dunes National Lakeshore and State Park

Comparisons Among Sites

Ordination and cluster analysis identified similar successional stages among the different study sites. This allowed separation of upper beach, foredune, mid- and late-successional blowout, sand prairie, and dunefield communities and habitats (Figure 6), which can provide correlation between Illinois Beach habitats and extant thistle population habitats in Indiana and Wisconsin.

Upper beach habitats from all three sites clustered together and shared relatively high sand cover. But *Cirsium pitcheri* was present in this habitat only at Kohler-Andrae (Table 1), which had the highest species richness and diversity of all upper beach sites, including many representatives of the upper beach association of Cowles (1899). Plot samples on the upper beach at Indiana Dunes were dominated by the single plant *Ammophila breviligulata*, while Illinois Beach had intermediate richness and diversity. However, most of the upper beach flora described by Gates (1912) was absent from the Illinois Beach plots, and the grass *Ammophila breviligulata* and the annuals *Euphorbia polygonifolia* and *Cakile edentula* were the dominant vegetation. Although not recorded separately, about half of the plants identified as *Ammophila breviligulata* at Illinois Beach were apparently the morphologically similar exotic grass *Elymus arenarius*.

The foredune at Illinois Beach clustered with the Indiana foredune and one Indiana blowout that supported *Cirsium pitcheri*. However, only three native species (*Ammophila breviligulata, Calamovilfa longifolia*, and *Cakile edentula*) were sampled at the Illinois site. The Indiana foredune supported ten species and differed from the blowout by the absence of *Cirsium pitcheri* and presence of the shrubs *Prunus pumila* and *Rhus aromatica*; the vine *Vitis riparia*; and the herbs *Artemisia caudata, Solidago racemosa*, and *Cakile edentula*.

Other Indiana blowouts clustered into mid- and late-successional groups along the second DECORANA axis. The mid-successional blowouts supported *Cirsium pitcheri* and clustered with the Illinois second dune. Sand cover exceeded 70% in these habitats, and the Illinois site differed primarily by lower relief and the presence of *Liatris aspera, Koeleria macrantha*, and *Asclepias tuberosa*. The late-successional blowout habitats all occurred in a 30-ha Indiana Dunes blowout complex and were distinguished by greater frequencies of the grasses *Andropogon scoparius* and *Calamovilfa longifolia*, and lower frequencies or absence of *Cirsium pitcheri*.

Although they were similar in species richness, diversity, and coarse structure, the Wisconsin and Illinois dunefield habitats clustered separately owing to differences in species composition and dominance. In Wisconsin, this habitat had 65% open sand with comparatively high cover from the grasses *Calamovilfa longifolia* and *Agropyron dasystachyum* and a shrub matrix of *Juniperus horizontalis* and *Prunus pumila*. The Illinois dunefield differed by having >75% sand, lower grass cover from *Andropogon scoparius* and *Calamovilfa longifolia*, prairie species such as *Liatris aspera* and *Petalostemum purpureum*, and the presence of *Arctostaphylos uva-ursi* in the shrub zone.

In Illinois, sand prairie vegetation in swales and on the second dune habitat clustered separately as late-successional sand prairie. This habitat had <60% sand cover and higher grass cover, species richness, and diversity than at Indiana or Wisconsin sites.

Habitat Selection for *Cirsium pitcheri* Reintroduction

Potential restoration habitat for *Cirsium pitcheri* in Illinois was identified by comparing similarities and differences in community stuctures and disturbance regimes between Illinois habitats and their analogues with extant thistle population habitats in Indiana and Wisconsin. In the Illinois upper beach, the comparatively low species richness and absence of perennial species (Figure 4) suggests that high sand erosion and replenishment rates might

Table 1. Species frequencies, species richness, and species diversity (H'), for habitat sampling transects in Illinois (IL), Indiana (IN), and Wisconsin (WI) Lake Michigan dune systems. Species and stands arranged by DECORANA and Ward's cluster analysis in relation to a successional gradient. DF = dunefield, SP = sand prairie, SD = secondary dune, BO = blowout, FD = foredune, UB = upper beach. Asterisks (*) indicate blowouts clustered as late successional on the second DECORANA axis (see Figure 6).

	ADVANCED SUCCESSION					MID/LATE* SUCCESSION								EARLY SUCCESSION						
SPECIES	ILDF	ILSP	ILSP	ILSP	ILSP	ILSD	INBO	INBO*	INBO	INSD	INBO*	WIDF	INBO*	INBO	INSD	INFD	WIUB	ILFD	ILUB	INUB
Asclepias verticillata		5																		
Aster pilosa		5																		
Aster ptarmicoides		15																		
Muhlenbergia mexicana		5																		
Polygonum sp.		5																		
Salsola sp.		5																		
Petalostemum purpureum	4	45	10	5																
Poa compressa		15	5																	
Arctostaphylos uva-ursi	24	25	25	5																
Coreopsis lanceolata		15		5																
Euphorbia corollata	28	10				10														
Liatris aspera	32	65	20	15		10														
Arenaria stricta		10		5																
Rosa carolina	4		5																	
Juniperus horizontalis	72											20								
Pinus nigra			5	5																
Koeleria macrantha		10	50	45		5						5								
Opuntia humifusa	4	5		15				5												
Asclepias tuberosa				5		5														
Elymus canadensis				10					5											
Sorghastrum nutans					5															
Solidago nemoralis	8	18	50	90	50		5	40	5	5			25		10					
Equisetum hyemale			5	65	60				5					5					5	
Smilacina stellata						15						5								
Asclepias syriaca					5	5				15										
Panicum sp.						5	5		5											
Festuca sp.							5													
Monarda punctata							15													
Pteridium aquilinum							10													
Saponaria officinalis							15			20										
Oenothera biennis						5						5								
Artemisia caudata		40	20	65		5	35	45	30	40	15	10	30	30		5	5			
Andropogon scoparius	56	85	100	90	100	65	70	100	85	80	50		100	75	30	40				
Panicum virgatum											5									
Solidago speciosa											5									
Calamovilfa longifolia	28	60	45	70	85	70	80	85	70	100	55	100	85	40	40	25	5	15		
Euphorbia sp.												5								
Cirsium pitcheri							10	15	25	50	5	35		10	10		5			
Prunus pumila	8	5	10			5	10		5			30		5		20	5			
Solidago racemosa									5	20	5		5	15		5				
Arabis lyrata							10		5				100	50						
Corispermum hyssopifolium				5				45	15	5	30		65	50	5		20	12		
Lithospermum caroliniense			5		5	5		15					5		25	5				
Agropyron dasystachyum												20					10			
Vitis riparia								5								10				
Rhus arenaria																5				
Lathyrus japonicus																	30			
Ammophila breviligulata												5	20	75	90	100	45	100	60	50
Cakile edentula																25			27	
Euphorbia polygonifolia																		15	40	
Salix sp.																			5	
SPECIES RICHNESS	11	20	14	16	7	13	12	9	12	9	8	11	9	10	7	10	8	3	6	1
SPECIES DIVERSITY (H')	2.02	2.55	2.18	2.52	1.53	1.92	2.01	1.86	1.89	1.84	1.66	1.85	1.87	2.02	1.59	1.80	1.66	0.70	1.46	0.00

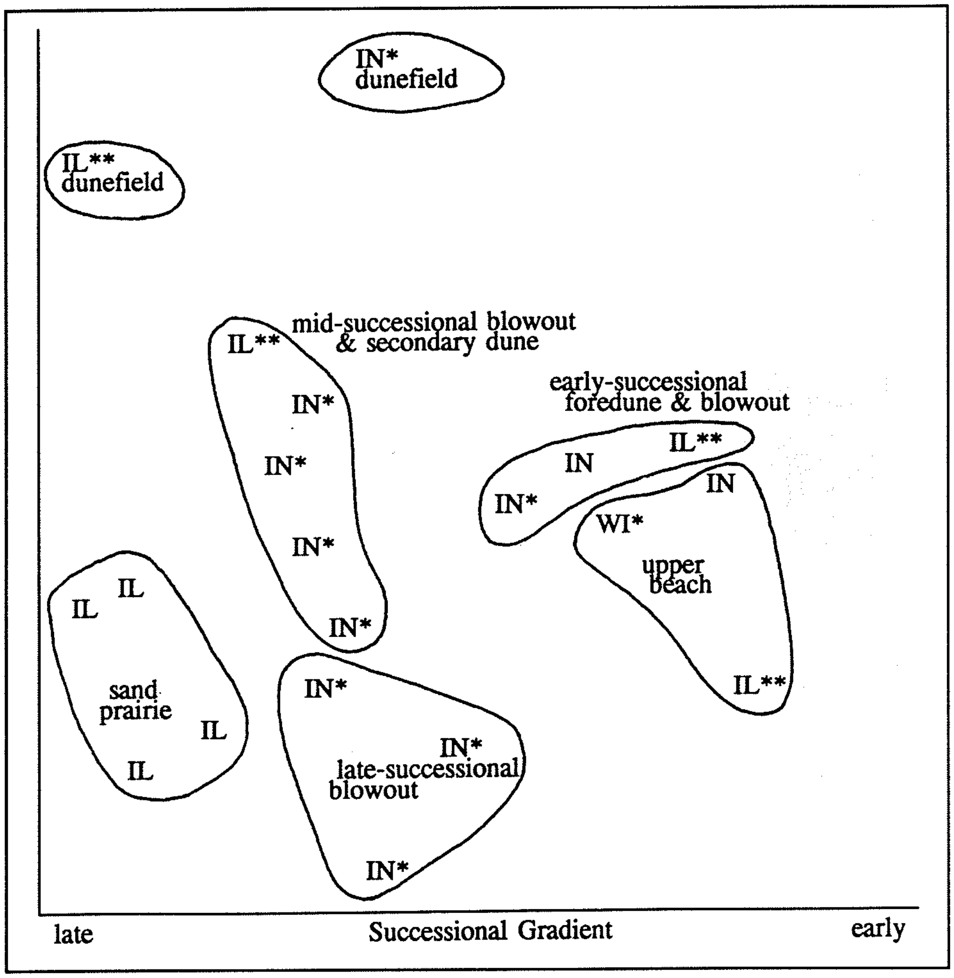

Figure 6. Distribution and successional patterns of southern Lake Michigan shoreline plant communities along a successional gradient inhabited by *Cirsium pitcheri*. IL = Illinois Beach State Park, IN = Indiana Dunes, WI = Kohler-Andrae State Park, * = *C. pitcheri* present, ** = potential *C. pitcheri* reintroduction site. Stands ordinated by DECORANA and clustered (within circles) by Ward's method (see text).

limit thistle survival. The Illinois foredune is also subject to frequent erosion, has comparatively low species richness, and has a high cover of rhizomatous grasses that might compete with thistles. The Wisconsin and Illinois dunefields are receiving recreational impact that may maintain appropriate disturbance patches for *Cirsium pitcheri*. However, the relatively low grass cover in the Illinois dunefield suggests that it is undergoing more intense recreational use than the Wisconsin site, which could impact thistle seedlings and limit their survival. The secondary dune habitat at Illinois Beach State Park clustered with early successional blowout habitat at Indiana that supported thistle populations and was essentially free from shoreline erosion, heavy grass competition, and recreational impact. This site was chosen for the initial thistle reintroduction.

RESULTS OF THISTLE PROPAGATION AND ESTABLISHMENT

Seedling and Planting Transect Characteristics

Forty Indiana seedlings and 37 Wisconsin seedlings were successfully propagated in the greenhouse. The Indiana seeds germinated a few days earlier than the Wisconsin seeds and developed broad cotyledons ($\bar{x}$ = 0.758 ± 0.079 mm) that were significantly wider (t = 11.79, p <.001) than those of the Wisconsin plants ($\bar{x}$ = 0.486 ± 0.055). This suggests that there were genetic differences between seed collection sites, although maternal effects cannot be ruled out. Nevertheless, the seedlings developed at equal rates in the greenhouse and were similar in mean leaf number (IN = 4.5 ± 0.82, WI = 4.9 ± 1.39), and mean leaf length (IN = 11.5 ±3.31, WI = 11.80 ± 3.86) when they were transplanted.

The planting transects (Table 2) were similar in overall community structure to the Illinois Beach secondary dune transect (Figure 4) that ordinated and clustered with mid-successional blowout habitat supporting thistles in Indiana (Figure 6). Thus the restoration was in a habitat analogous to thistle habitat in Indiana. In addition, the planting transects did not significantly differ from each other in vegetative composition, (H' = 0.26, P >.95). They had >70% sand, and the grasses *Andropogon scoparius, Calamovilfa longifolia*, and *Koeleria macrantha* and forbs *Liatris aspera* and *Solidago nemoralis* were dominant in them (Table 2). Thus, community structural differences that might affect thistle survival were absent between transects.

First-year Survivorship

By late May 1992, 29.9% (23 plants) of the 1991 planting cohort were alive and continued to survive through the 1992 growing season. There was an unexpected significant difference (X^2 = 5.89, p = .016) in survival between the first and second planting transect (both contained mixed seed sources), with 13% and 50% survivorship, respectively. No significant differences in survival occurred between the east and west halves of the planting transects, either with Wisconsin or Indiana plants. Among all transects, the seed sources had significantly different survivorship (X^2 = 6.14, P = .014), with 45% of the Indiana plants and 16.2% of the Wisconsin plants alive (Figure 7). Although a greater percentage of fenced (45.8%) vs. unfenced (33.3%) Indiana plants survived, the proportions were not significantly different. Survivorship was about 15% for Wisconsin seedlings, whether they were fenced or unfenced. Herbivory was not apparent in any surviving plants, either in September 1991 (J. Schwegman, pers. com.) or in May 1992. Thus mortality may have been a function of plant vigor and apparently occurred over the winter.

Table 2. Ranking of species and substrate by importance values, and summary of community structure of *Cirsium pitcheri* reintroduction transects at Illinois Beach Nature Preserve.

	TR #1	TR #2	TR #3	TR #4
Sand	95.15	96.13	93.20	95.73
Andropogon scoparius	36.10	30.50	28.32	33.20
Calamovilfa longifolia	28.34	17.03	31.06	23.67
Liatris aspera	18.20	17.35	19.33	5.81
Koeleria macrantha	6.00	13.20	11.53	12.07
Solidago nemoralis	6.11	6.50	5.04	11.84
Petalostemum purpureum	4.28	5.72	—	—
Poa compressa	—	2.94	1.93	4.99
Panicum virgatum	—	4.04	—	3.02
Elymus canadensis	—	—	4.17	0.99
Opuntia humifusa	1.14	2.08	1.46	—
Equisetum hyemale	—	—	—	3.80
Euphorbia corollata	—	3.64	—	—
Sorghastrum nutans	—	—	1.86	1.51
Liatris cylindrace	2.01	—	—	—
Prunus pumila	1.54	—	1.10	—
Corispermum hyssopifolium	—	—	0.94	0.95
Artemisia caudata	—	0.86	—	0.95
Lithospermum caroliniense	—	—	—	0.99
Unknown herb	1.14	—	—	—
SUMMARY				
% sand cover	71.0%	75.6%	70.6%	73.0%
Sand IV	95.15	96.13	93.20	95.73
Total grass IV	70.44	67.71	78.87	79.45
Total forb IV	32.87	35.16	26.83	24.82
Total shrub IV	1.54	0.10	1.10	0.0
Species richness	10.00	11.00	11.00	13.00

DISCUSSION

Site Selection

The potential for reintroduction of *Cirsium pitcheri* to Illinois Beach extends across a habitat continuum inland from the Lake Michigan shoreline. The habitat criteria of ≥ 70% open sand for *C. pitcheri* occurs on the upper beach, foredune, dunefield, and secondary dune, each of which are ecologically analogous to extant thistle population habitats in Indiana or Wisconsin. However, various human impacts may limit restoration success on these narrow, linear habitats. Although frequent beach erosion and foredune erosion are alleviated by artificial sand replenishment, the erosion process may exceed frequency and severity thresholds for thistle establishment and persistence. Similarly, recreational use of the dunefield may create potential thistle habitat, but trampling might negatively impact seedling or juvenile thistles. Thus, the secondary dune at Illinois Beach was chosen as optimum habitat for thistle reintroduction because the open sand is maintined by natural processes and the site is protected from shoreline erosion and human impact.

Survivorship

If the difference in cotyledon size between Wisconsin and Indiana seed sources is genetically based and related to the significant negative correlation in genetic similarity that Loveless and Hamrick (1988) found with increasing distance between populations of *Cirsium pitcheri*, then the 150-km distance between seed sources is apparently great enough for such differentiation. Although the survivorship differences between seed sources may have been coincidental, owing to small sample size, there are several alternative scenarios. One possible explanation is a genotypic difference, as the Indiana seed source is 70 km closer to Illinois Beach than the Wisconsin seed source. Whereas the low Illinois and Wisconsin shoreline dune systems might appear more ecologically similar than the high inland blowouts at Indiana, the more southern Illinois and Indiana habitats may require thistles adapted to more xeric habitats. Although the mixed mating system of *C. pitcheri* should accommodate some inbreeding, selfing lowers seed set (Loveless 1984) and might have affected the vigor of Wisconsin plants. For example, Dudash (1990) found less inbreeding depression in greenhouse and garden environments than in natural habitat for *Sabatia angularis*. Thus, the nearly identical size of the Indiana and Wisconsin plants at the time of planting could have been the result of greenhouse propagation, and over-winter mortality might then have expressed inbreeding depression among the Wisconsin plants.

Although differences in survivorship occurred between the two transects that supported mixed Indiana and Wisconsin plantings, this could have resulted by chance. A more expected result would have been a difference in survival between the west and east halves of the transects, as they crossed an environmental gradient between dune top and dune slope. Although no such differences occurred either with Wisconsin or Indiana plants, these effects may be expressed in performance over time. The lack of a significant difference between fenced and nonfenced survivorship suggests that herbivory should not be an important factor affecting thistle survival. Thus demographic differences among individual plants should be the primary focus of continued monitoring.

Population Development

Development of a successfully reproducing *Cirsium pitcheri* population at Illinois Beach will require establishment of a staged cohort structure, thereby ensuring that reproductive failure of a single cohort does not result in loss of the entire population.

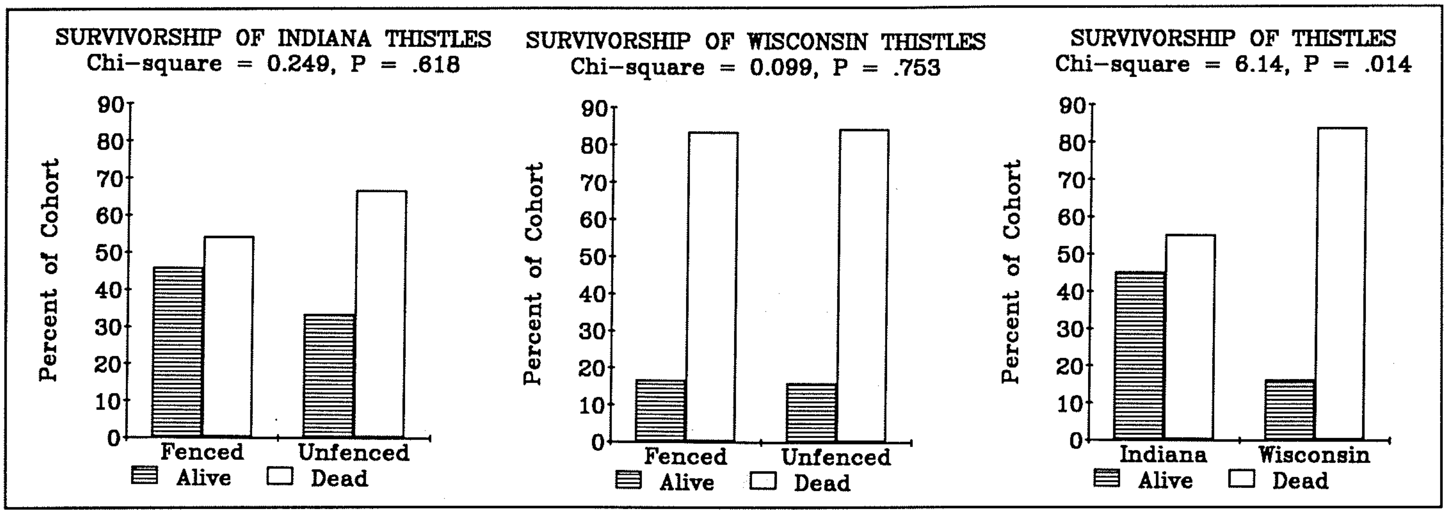

Figure 7. Comparison of survivorship between fenced and unfenced Indiana (left) and Wisconsin (center) *Cirsium pitcheri* cohorts, and between fenced and unfenced Indiana and Wisconsin cohorts (right) established at Illinois Beach State Park, Lake County, Illinois.

As individual plant growth rates adjust to microhabitat differences (sensu Loveless 1984), planted cohorts should diverge, increasing cohort diversity while decreasing the number of plants that might simultaneously reach reproductive maturity. Continued recovery should focus on establishing additional larger cohorts and ensuring a staged population structure across the secondary dune, thereby buffering the population against loss due to wide-scale demographic effects (Goodman 1987a), and enhancing the potential for population persistence if this gradient shifts in time and space.

The strategy of planting greenhouse-propagated plants avoids effects of seed predation and environmental stress on seedlings, and may reduce thistle mortality, thereby maximizing cohort size and possibly accelerating rates of maturity. However, greenhouse propagation avoids environmental selection at the seed germination stage (Pavlik 1993) and may allow persistence of poorly adapted plants. Thus, experimental seed dispersal will be used to supplement the plantings and further test effects of seed source and microhabitat on seedling survival. Once members of the initial cohort reach reproductive maturity, we plan to use experimental insecticide treatment of flowering plants to deter seed predators (sensu Louda 1993), and to harvest and plant seeds to enhance seedling establishment and population growth.

Metapopulation Development

Establishing a single population in one area at Illinois Beach is the first step in restoring a metapopulation that can persist as lake levels and dune habitats change (McEachern et al. 1993). Although the initial secondary dune population may shift spatially as lake levels fluctuate, it remains vulnerable to local disturbance. Therefore, establishing additional independent populations is critical to restoring a metapopulation to Illinois Beach. The dunefield at Illinois Beach is potential habitat for a spatially isolated second population. If populations can be restored in the dunefield and thistle migration occurs along the approximately 1000 m of beach and foredune connecting the dunefield and secondary dune, the beginnings of a functioning metapopulation may be established at Illinois Beach. Successful metapopulation maintenance will require further experimentation and management. This should be based on evaluating the impact of recreation on thistles in dunefield habitat and monitoring impacts of beach erosion and replenishment rates on thistle colonization of upper beach and foredune habitats.

CONCLUSIONS

Restoration of disturbance-dependent plant species demands an understanding of their natural habitat dynamics, ecological requirements, life-history strategies, and responses to natural and anthropogenic disturbance regimes (Pavlovic 1993), as well as resolution of factors affecting their successful establishment (Pavlik 1993, Pavlik et al. 1993). Through plant community ordination and gradient analysis we identified the secondary dune system at Illinois Beach as optimum reintroduction habitat for *Cirsium pitcheri* that avoided anthropogenic disturbance. However, experimentation will be required to identify optimum microhabitats for successful establishment of populations. Interpreting demographic responses to the scale and frequency of shoreline erosion, beach replenishment, and recreational impact will be a key to restoration at the metapopulation scale.

It may be necessary to use several reintroduction strategies to establish *Cirsium pitcheri* at Illinois Beach in order to overcome extinction thresholds and allow colonization of new habitats. Planting greenhouse-propagated juvenile thistles should maximize cohort size and accelerate maturity and reproduction, and thus help overcome extinction thresholds associated with small populations. However, experimental seed planting will be required to allow selection to operate at the seedling stage, thereby optimizing local adaptation of the restored population. A critical stage in the restoration will occur when initial cohorts reach reproductive maturity. Protection from seed predation, and supplementary seed harvest and propagation, may be required to bolster seed production and seedling establishment, allowing population maintenance and colonization of new habitats.

Ensuring *Cirsium pitcheri* metapopulation persistence at Illinois Beach may require continued supplemental thistle establishment, regulation (but not necessarily elimination) of recreational use, and both control and amelioration of beach erosion processes. This reflects the hierarchical strategy of Goodman (1987b) for preventing species extinction by (1) manipulating reserve design, (2) enhancing habitat and resources, and (3) augmenting populations of the target species. It may be a necessary recipe for recovery and restoration of species in a global environment that can no longer escape human impacts.

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